Notes on the Larval Skeleton of Spatangus purpureus.

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With Plate 21.

ALTHOUGH 'one of the very first Echinoderms of which artificial fertilization and rearing of the larvae were undertaken' (Mortensen, **6**, p. 14), the development and especially the structure of the larval skeleton of Spatangus purpureus have been rather imperfectly known. Krohn's descriptions and figures (**2**, **3**) are not quite satisfactory with regard to the skeletal structure. and. moreover. the larvae described in his second paper are doubtful as to their specific identification (Mortensen, **6**, p. 15). Through Mortensen's renewed observations on the artificially-reared larvae of this species (**6**, pp. 14–17) the external features of the larval development are now made clearer. As to the larval skeleton, however, he was only able to give some brief information owing to the unfortunately bad state of preservation of his specimens. Among other Spatangoids, Echinocardium cordatum and Brissopsis lyrifera were carefully studied by Macbride (**4**) and Mortensen (**7**, pp. 144–8), and the larvae of these three species have been shown to have such a striking resemblance to each other in early stages that it is desirable to ascertain some more minute diagnostic characters for each species. In such circumstances it seems not unnecessary to put on record detailed descriptions of the skeletal structure of the larva of Spatangus purpureus.

The material on which my work is based consists of a series of larvae, reared and preserved by Mr. Elmhirst at Millport, and kindly handed over to me for study by Professor E. W. MacBride.[1] Although there are found several gaps in developmental stages, the changes undergone by the larval skeleton could be followed fairly satisfactorily. From the labels which were found attached to the vials we obtain the following chronological accounts.

The earliest stage which is represented by segmenting eggs is dated 16th May 1914. This is probably the day on which the eggs were artificially fertilized. The further stages with regard to the age in days are:

2nd day	May 17th . .	Blastula.
3rd ,,	,, 18th . .	Gastrula.
4th ,,	,, 19th . .	Young 2-armed pluteus.
5th ,,	,, 20th . .	Fully-formed 2-armed pluteus.
6th ,,	,, 21st . .	4-armed pluteus.
17th ,,	June 1st . . .	6-armed pluteus.
?	? . . .	8- or 10-armed pluteus.
24th ,,	June 8th . .	12-armed pluteus.

Thus in full accordance with the statements of Mortensen (**6**, p. 15) the larva reaches its last stage in the course of three weeks. It is to be regretted that those larvae whose skeleton was best preserved had been kept together in one vial, all the different stages being mixed up, and without any label, so that it is not possible to give a chronological state-

[1] The present work was done partly in the zoological laboratory of the Imperial College of Science and Technology and partly in the British Museum (Natural History). My cordial thanks are due to Professor E. W. MacBride of the College and to Sir Sidney F. Harmer of the Museum, for help and encouragement in various ways and for the privilege of the use of the laboratory and the libraries.

ment in most cases as regards the first appearance of a new calcification centre or its subsequent development, &c.

At the outset I may call attention to the fact that the latticed rods, viz. the postoral, postero-dorsal, and posterior unpaired (so-called aboral spike), are morphologically different from the other simple, though often thorny, rods which serve equally as the support of each corresponding arm. Théel (**11**, pp. 40–1) described very clearly the early development of the postoral rods of Echinocyamus pusillus as follows: 'they (the latticed rods) begin to arise during the gastrula stage as three small processes, one on each rod of the star close to its centre, Pl. iii, fig. 38. These processes stretch in length, run parallel and become connected by transverse beams'. The same is exactly true for the corresponding rods and also for the other latticed rods in Spatangus. In all of these a three-rayed 'star' is first laid down lying parallel to the surface of the body. From each of the rays or arms, very close to the centre, is given out a vertical process, directed towards the surface of the body. The latter, three in number if, as in most cases, all developed, give rise to a latticed rod. The postoral and postero-dorsal rods of Echinocardium cordatum are both stated by MacBride to be formed of only two parallel rods (**4**, pp. 475, 477). As compared with the table-like calcareous body, which is commonly met with in all classes of Echinoderms, the latticed rod corresponds to the spire, and the three-rayed portion to the base. Thus the above-named two-paired and one unpaired latticed rods are morphologically composite in structure and are from the beginning directed vertically to the surface of the body. On the other hand, those rods supporting the antero-lateral and postero-lateral arms are morphologically simple, being produced either as prolongations or branches of the three-rayed base, which were lying originally parallel to the surface of the body. The body-, recurrent, and horizontal rods are also either prolongations or branches of the basal part, which remained running along the surface of the body without, however, pushing out to support arms. The dorsal arch consists only of the three-rayed portion, from which any vertical process fails to develop. The pre-oral and antero-dorsal rods also belong, according to this interpretation, to the simple type of the rods. In a similar manner, it seems to me, in Arbacia, Dorocidaris, Echinocyamus, &c., the posterior unpaired star fails to produce vertical processes, which would give rise to the aboral spike in the Spatangoid larva, the laterally directed basal arms being only developed as the postero-lateral rods. Prouho's discovery of an abnormal larva of Dorocidaris papillata which produced a well-developed aboral spike (**10**, pp. 349–50, Pl. xxv, fig. 9; cf. Mortensen, **5**, p. 75) is exceedingly interesting in this respect. Mortensen (**5**, p. 71) maintains that the statements of some authors, e.g. Kölliker's, who have described plutei with six to ten latticed rods must be wrong. My observations confirm this conclusion. Though in some abnormal cases those morphologically simple rods may be doubled or split, analogous to those I have observed, e.g. the dorsal horizontal rod of the right side (Pl. 21, figs. 7 and 8, *dh*) and the left recurrent rod (fig. 6, *re*), it is quite impossible that they should assume latticed structure.

Late in the gastrula stage a pair of calcification centres appear, which are bilaterally symmetrical in position. This state of affairs is so well known in other Echinoids that any detailed description is quite unnecessary. I may, however, point out that the body-rod represents one of the three-rayed basal arms, not simply a posterior continuation of the postoral rod, as might easily be wrongly inferred because they both run in an almost straight line (fig. 1, *br*, *po*). The other two arms of the base are represented respectively by the ventral horizontal rod (*vh*) and the recurrent rod (*re*), from which latter the antero-lateral rod (*al*) is given out later.

The third, unpaired calcification centre appears near the posterior end of the body (*ab*). This may appear as early as in the stage where the future postoral arms can as yet hardly be recognized as arms, viz. when the larva has formed a slight concavity at the oral field and has begun to assume roughly a tetragonal shape. The star is situated in such a position that two of its arms lie bilaterally and the remaining one is directed dorsally. The former two ultimately give rise to the postero-lateral rods, while the third remains as a short but distinct spur-like process all through the larval life (figs. 3–8). From each of these arms a vertical process is produced, directing posteriorly. These three vertical processes form together the aboral spike (fig. 2, *ab*). Being robust in structure the transverse beams extend rapidly so as to obliterate the openings between them.

Hand in hand with the rapid growth in length of the post-oral rods the arms of the basal portion develop to assume their future position. The body-rods, which run straight postero-medially, are the most rapid in growth among them, and their posterior ends come to overlap each other (fig. 1, *br.*). In the corresponding stage as well as later, as figured by Krohn (**2**, Pl. vii, figs. 1–3, 6), the posterior ends of the body-rods are shown standing fairly apart. Except in a later stage where the rods begin to be absorbed at the posterior ends (figs. 5 and 7), I have never met with such a state as shown in his figures. The second arm, the recurrent rod (*re*), which is at first directed dorsally, soon bends posteriorly. In the meantime it produces a branch at its bent portion. This branch, which is the future antero-lateral rod (*al*), proceeds a little towards the median line, but soon bends anteriorly to run almost parallel to its fellows of the other side, though slightly approaching this as it runs. Its base is a little broadened and bears a few minute processes, as shown in Krohn's figure (**2**, Pl. vii, fig. 5, *c*) and confirmed by Mortensen (**6**, p. 15). The remaining arm of the first calcification centre runs along the ventral surface, almost transversely towards the median line, but slightly deviating anteriorly (fig. 1, *vh*). This is the ventral horizontal rod. The end soon comes in contact with that of its fellow of the other side, and they ultimately fuse, forming a characteristic thickened joint (figs. 2 and 3, *vh*). This feature is constantly seen and lasts for a fairly long period, and it seems to me that this can be regarded as a specific character in identifying Spatangoid larvae. In many other Spatangoid larvae this is not the case; these rods either stand apart or pass across, as in Echinocardium cordatum and its doubtful ally (Müller, **8**, p. 290, Pl. iii, fig. 2). In cases where both ends come very close together, as in Echinopluteus fusus (Müller, **9**, Pl. vii, fig. 2), E. solidus (**9**, Pl. vi, fig. 9; Pl. vii, fig. 1), and perhaps Brissopsis lyrifera also (Mortensen, **7**, fig. 2), they do not form any thickened joint. Only in Chadwick's figures of an unidentified form (**1**, Pl. ix, figs. 61 and 62) the similar state of the ventral horizontal rods is very clearly shown.

By the time when the two-armed stage is fully developed, when the post-oral arms have reached the length nearly equal to the body proper, whereas neither the antero-lateral arms nor the aboral process are as yet distinct, the following features are to be noticed: the post-oral rods are usually solid and three-ridged, and the margin of the ridges is not serrated. Exceptionally, however, some irregularly-scattered holes may be met with even near the proximal end of the rod, but owing to the very slight differences in the refractive indices between the thin, filmy skeleton and the surrounding medium, which consists of oil of cloves or Canada balsam, it is difficult to demonstrate the holes clearly. Krohn (**2**, p. 256) observed no fenestration in these rods in the corresponding stage. Further, in his figure (Pl. vii, fig. 1) he showed only the antero-lateral and body-rods besides the post-oral, whilst the ventral horizontal and recurrent rods are not represented. The star of the aboral spike should also have appeared in this stage.

The recurrent rod grows rapidly, and when its posterior end comes in contact with that of its fellow of the other side (fig. 2, *re*) fuses with it and increases in thickness, often being beset with some irregular short processes near the end (fig. 3, *re*). A little anterior to this end a branch is soon sent out ventrally, while about the same time the body-rod produces a branch dorsally, and these two branches meet and fuse midway between the body- and recurrent rods (figs. 4 and 6, *c*). There are very often some irregular spines or branches from the dorso-ventral connexion thus formed. As the result of this connexion there is formed a rectangular framework as seen from side (cf. Mortensen, **5**, p. 75, Pl. ix, fig. 9). From the point where the antero-lateral rod diverges from the recurrent rod there is formed frequently a short process directed anteriorly (figs. 2 and 6). This seems to have no significance.

Lastly, at the end of the two-armed stage the body-rods fuse at the point where they have been overlapping each other, so as to form an oblique cross. Very often there is formed an accessory connecting-span between the two body-rods. This is a short transverse piece lying a short distance anterior to the crossing-point. Now the calcareous framework encircling the stomach has become fairly rigid. The body-, recurrent, and ventral horizontal rods of both sides are fused in the median plane with the respective fellow of the other side, while, on the other hand, the body- and recurrent rods are connected with each other near the posterior end on each side of the body.

After having reached this state the body-rod increases no longer in length, so that, as long as its posterior end remains unabsorbed, its length can be taken as unit in describing the dimensions of other parts. The length of the body-rod can easily be measured when the larva is laid with its ventral side downwards, so that the rod is seen in its real length without foreshortening. As expressed in terms of the ratios to the body-rods, the post-oral rod reaches during the two-armed stage a length more than twice as long as the body-rod, the antero-lateral rod more than one-half, and the aboral spike about one-third.

The aboral process and the antero-lateral arms become discernible almost simultaneously. It may now be called the four-armed stage (figs. 3–5). The change which takes place during this stage is the enormous increase in lengths of the post-oral and antero-lateral rods and of the aboral spike.

The post-oral rods grow up to four or five times the length of the body-rod, while the antero-lateral rod and the aboral spike reach more or less twice the length of the same (fig. 5).

The post-oral rods seem in most cases to be devoid of fenestration in their proximal half or one-third, whereas the unfenestrated portion of the aboral spike is generally much shorter. In an extreme case in the latter the fenestration begins close to the proximal end (fig. 6, *ab*), exactly as the feature seen by Krohn in an unidentified form (**3**, p. 210). The distal parts of these rods are fairly regularly serrated. The serration seems to begin roughly at the point where the fenestration also begins (fig. 5, *po*, *ab*). The posterior ends of both the body- and recurrent rods show towards the end of this stage signs of degeneration, being gradually absorbed. The dorsal arch makes its appearance near the end of this stage, on the mid-dorsal line at the level where the oesophagus opens to the stomach (fig. 5, *da*). The two arms of the star, which lie symmetrically and are directed antero-laterally, increase rapidly in length, while the unpaired, posteriorly-directed arm remains very short, sometimes even obliterated.

Krohn's figure (**2**, Pl. vii, fig. 2) corresponds to the early four-armed stage. It is the dorsal view, in which the ventral horizontal rods and the body-rods are not shown, while the descending rods, which I take as the recurrent, are not coming to meet each other at the posterior ends. The post-oral rods are shown as fenestrated on their distal three-fifths, while the aboral spike remains unfenestrated. Both these kinds of rods are, however, shown to have serrated edges along their whole length.

The next, six-armed stage, is characterized by the appearance of the postero-dorsal arms. Previous to the appearance of these arms the supporting skeleton, which is called the postero-dorsal rod, is formed underneath each of them (fig. 6, *pd*). The rod develops in the manner similar to that of the other latticed rods, and as described and figured by Théel in Echinocyamus pusillus (**11**, p. 44, Pl. vi, fig. 88, *y*). The arms of the star lie in such a position that one is directed anteriorly, another postero-laterally, and the remaining one postero-medially. From the lack of adequate material the fate of the former two arms cannot be stated with certainty, though it seems probable that they do not develop much farther. The postero-medially-directed arm in the later stages continues to develop in a direction parallel to the dorsal surface, reminding one of the body-rod on the ventral side (figs. 7 and 8). Near the base of this arm a branch is sent out in an antero-median direction, reminding one again of the ventral horizontal rod. This is the dorsal horizontal rod (*dh*). From each of the arms of the star, close to the centre, is given out a vertical process, very often differing in the rate of development, but ultimately the three in all give rise to the latticed postero-dorsal rod.

Although from want of material, especially of the later part of this stage, no definite statement can be made, yet, judging from later specimens, it is highly probable that the post-oral rod increases in length during the six-armed stage up to nearly 6 times the length of the body-rod, the antero-lateral rod 3 times, the aboral spike nearly 3·5 times, and the postero-dorsal rod probably at least 1·5–2 times the length of the same.

In Krohn's figure (**2**, Pl. vii, fig. 3) is indicated the three-rayed base of the postero-dorsal rod (*e*). The buds of the pre-oral arms have already appeared (*d*), while the dorsal arch is still in a rudimentary condition, of which, however, nothing is mentioned. The fact that the pre-oral arms appear without any mechanical influence of the underlying skeleton is also seen in Echinocardium cordatum (**4**, p. 477, Pl. xxxiii. fig. 6). But both in MacBride's case of Echinocardium and my specimens of Spatangus the appearance of the pre-oral arms takes place much later than the stage as shown by Krohn, viz. even when the postero-dorsal arms have attained a fair length, there was as yet no sign of these arms found. Krohn gives some detailed structures in a somewhat advanced six-armed stage (Pl. vii, figs. 5 and 6). If the fig. 5 is really the dorsal view, as stated by him, then the dorsal arch (*d*) should lie above the antero-lateral rods (*c*). The two arms of the base of the postero-dorsal rod (*f*, *g*) are shown very well developed, and that the serrated recurrent rods meet each other at the broadened posterior ends is also clearly drawn. His fig. 6, which is the ventral view, is somewhat difficult to understand. There are two sets of rods which seem to correspond to the ventral horizontal rods, both overlapping each other at the end. Whether it is really an abnormal case, as in the right dorsal horizontal rod in my oldest larva (figs. 7 and 8, *dh*), or due to his misrepresentation cannot be decided at present.

The further advanced stages are represented by a small number of eight- to ten-armed larvae with dissolved skeleton, and a single specimen of the twelve-armed stage.

The fourth pair of arms to appear are the pre-oral, which are supported respectively by the direct prolongations of each end of the dorsal arch. The fifth pair are the postero-lateral, supported by the lateral prolongations from the base of the aboral spike. From want of material showing any adequate stage I cannot decide whether the postero-lateral arms have from the beginning a skeletal support, as e.g. in Echinocardium cordatum (MacBride, **4**, p. 479), or not, as e.g. in Brissopsis lyrifera (Mortensen, **7**, pp. 147–8). Judging, however, from the fact that the arms soon develop to assume their typical shape, instead of remaining as ear-shaped lobes, I am strongly inclined to think that the arms in question of Spatangus purpureus do contain their skeletal support from their earliest stage.

Owing to the remarkable increase in size of the stomach during the eight to ten-armed stage, that skeletal framework which formerly encircled the stomach must have undergone corresponding changes. This can be judged from the state seen in the twelve-armed specimen (figs. 7 and 8). Both the body- and recurrent rods are shortened at the posterior ends, their side-by-side connexion being broken. The ventral horizontal rods of both sides are also separated from each other at the joint. This broken framework does not now encircle the stomach, but has gradually been pushed posteriorly, and the angles between the body- and recurrent rods of one side and their fellows of the other side are much widened.

The twelve-armed specimen (figs. 7 and 8) is much younger than the larva figured by Mortensen (**6,** fig. 14), the total length measuring only 2·1 mm. The pre-oral and postero-lateral arms are nearly equal in length, measuring 0·3 mm., a little shorter than the antero-lateral, which measure 0·35 mm. The antero-dorsal arms, which have appeared last, are only in the form of buds. The other arms and process are remarkably long, i.e. the posterior arms measuring 1 mm. in length, the posterior process 0·9 mm., and the postero-dorsal arms 0·8 mm.

A short distance anterior to the point where the antero-dorsal rod is sent out from the dorsal arch, the latter produces a short lateral branch. The same is noticed by Müller in Echinopluteus fusus (**9,** Pl. vii, fig. 3) and by Mortensen in Echinocardium cordatum (**5,** p. 103, Pl. ix, fig. 6). In a Spatangoid larva, which has been doubtfully identified by Mortensen (**5,** pp. 102–3) with Echinocardium cordatum, Müller described and figured a peculiar feature in that the median posterior branch of the dorsal arch fused with the tips of the dorsal horizontal rods (**8,** p. 290, Pl. iii, figs. 1 and 4, *d*). So far as I know such a case has never since been recorded by any other observers nor have I noticed it in my specimens (figs. 7 and 8, *da*, *dh*). The postero-lateral rod has no noticeable characteristics, being of a uniform thickness throughout and rather smooth, differing from the richly-serrated state as seen in Echinocardium cordatum (Mortensen, **5,** p. 103, Pl. ix, figs. 7 and 8; MacBride, **4,** Pl. xxxiii, fig. 11, *pla*).

The rectangle formed by the body- and recurrent rods as seen in some younger stages (figs. 4 and 6) can no more be found (fig. 8). The area roughly corresponding to the anterior half of the rectangle is now occupied by an irregularly-perforated calcareous plate, which is developed more strongly on the right side than on the left side. The bases of the post-oral (*po*) and antero-lateral rods (*al*) are incorporated into this calcareous plate, and the recurrent rod is now hardly distinguishable. Although it is difficult to make out clearly, it seems highly probable that neither the bases of the postero-dorsal (*pd*) nor of the postero-lateral rods (*pl*) are fused with that plate. Similar features in the formation of calcareous plates are frequently met with in other irregular sea-urchins, e.g. Echinopluteus fusus (Müller, **9**, Pl. iv, fig. 7; Pl. vii, figs. 3 and 11), Arbacia pustulosa (Müller, **9**, Pl. iii, figs. 2 and 3), &c. Whether these plates have anything to do with the definitive skeleton of the young sea-urchin is still an open question, though it seems probable that they are absorbed altogether at the time of metamorphosis.

Summary.

1. The larva of Spatangus purpureus reaches its last stage, which is characterized by its possession of six pairs of arms, in the course of three weeks after fertilization.

2. The paired arms develop in the following order: post-oral, antero-lateral, postero-dorsal, pre-oral, postero-lateral, and antero-dorsal. The posterior process appears about the same time as the antero-lateral arms become distinct.

3. These six pairs of arms and the unpaired process are each supported by a calcareous rod. Of these calcareous rods one can distinguish two classes which differ morphologically from each other, viz. the simple and the composite.

4. To the class of simple rods belong the antero-lateral, pre-oral, postero-lateral, and antero-dorsal rods. They are either direct prolongations or branches of the three arms produced from one of the calcification centres. They are originally horizontal (parallel to the surface of the body) in position, and are homologous with the body-, recurrent, and horizontal rods.

5. The remaining rods, viz. the post-oral and postero-dorsal rods and the aboral spike (posterior rod) are composite. They are each composed of three parallel rods connected by transverse beams so as to give a latticed appearance. Each

of the parallel rods is a branch given out vertically from an arm of the calcification centre.

6. The larval skeleton of Spatangus purpureus is characterized chiefly by (*a*) more or less considerable length of the unfenestrated proximal portions in the latticed rods, (*b*) fusion of the tips of the ventral horizontal rods forming a thickened joint, (*c*) overlapping of the body-rods near their posterior ends, and subsequent fusion of this part so as to form an oblique cross, (*d*) rather simple appearance of the postero-lateral rods, and (*e*) formation of a calcareous plate on each side of the stomach in the oldest stage.

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EXPLANATION OF PLATE 21.

(All figures were drawn by means of a camera lucida and magnified 200 times.)

Fig. 1.—Dorsal view of a young two-armed larva, in which the rudiment of the aboral spike (*ab*) has just appeared. (An unusually long process is seen arising from the base of the right post-oral rod.)

Fig. 2.—Dorsal view of an old two-armed larva to show the fusion at the tips of the ventral horizontal rods (*vh*). (The posterior ends of the body-rods, *br*, are not overlapping here as normally.)

Fig. 3.—Dorsal view of a young four-armed larva to show the fusion of the posterior ends of the recurrent rods (*re*). The body-rods (*br*) are also fused with each other (hidden behind the aboral spike, *ab*).

Fig. 4.—Left-side view of the same specimen as shown in fig. 3. A rectangle is formed by the body- (*br*) and recurrent rods (*re*). (From the base of the aboral spike an additional process is given out ventrally.)

Fig. 5.—Dorsal view of an old 4-armed larva, in which the rudiment of the dorsal arch (*da*) has appeared and the posterior ends of the body-rods have begun to degenerate.

Fig. 6.—Right-side view of a young six-armed larva to show the early stage of the postero-dorsal rod (*pd*). (The left recurrent rod, *re*, is here seen abnormally split into two.)

Fig. 7.—Dorsal view of a twelve-armed larva. The body- (*br*), recurrent and ventral horizontal rods (*vh*) have all lost their connexion with the fellows of the other side. (The right dorsal horizontal rod, *dh*, is abnormally doubled.)

Fig. 8.—Right-side view of the same specimen as shown in fig. 7, to show the calcareous plate formed between the body- (*br*) and recurrent rods.

Abbreviations.

ab = aboral spike ; *ad* = antero-dorsal rod ; *al* = antero-lateral rod ; *br* = body-rod ; *c* = dorso-ventral connexion between body- and recurrent rods ; *da* = dorsal arch ; *dh* = dorsal horizontal rod ; *pd* = postero-dorsal rod ; *pl* = postero-lateral rod ; *po* = post-oral rod ; *pr* = pre-oral rod ; *re* = recurrent rod ; *vh* = ventral horizontal rod.